



Perceived predation risk affects sleep behaviour in free-living great tits, *Parus major*



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Sleep is of major importance to most organisms but insights into how sleep is affected by ecological processes are largely lacking. Perceived predation risk constitutes a major factor that should shape adaptive phenotypic plasticity in sleep but it is unclear to what degree an individual can tailor sleep to different types of risk. If animals base behavioural decisions on the predation landscape then we would expect individuals to adjust their sleep behaviour when exposed to changes in predation risk. Here we investigated the plasticity of phenotypic sleep in wild great tits roosting in nestboxes and exposed to different types of predation risk. Following our prediction, when exposed to experimentally increased perceived predation risk from owls, *Strix aluco* (a bird that can prey on birds solely outside their roosting cavity), individuals increased total sleep duration. Contrary to our prediction, when exposed to experimentally increased perceived predation risk from martens, *Martes martes* (a mammal that can prey on birds inside cavities), individuals woke up less often during the night, but otherwise did not change their sleep behaviour. Birds did not alter total time spent awake during the night in response to predator exposure. Our findings demonstrate that individual great tits modify their sleep behaviour in response to changes in predation risk. Ecological factors including exposure to predators, resource availability and reproductive competition may act as significant constraints on natural sleep patterns and warrant further investigation with free-living individuals.

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Sleep is a requisite component of self-maintenance as it plays important roles in energy conservation (Siegel, 2005), cellular repair (Savage & West, 2007) and learning. Extended sleep deprivation leads to cognitive and physical impairment (Koslowsky & Babkoff, 1992) and, eventually, death. Organisms must allocate limited resources between self-maintenance and reproduction, making trade-offs between investment in multiple costly behaviours, such as foraging to gain energy or behavioural defence for survival. Sleep constitutes a prime example of a behavioural trade-off because sleep precludes active behaviours such as foraging, territory defence, mating, mate guarding and antipredator vigilance. As sleep plays a role in maintaining high levels of physical and cognitive performance, understanding variation in sleep patterns in the wild, and how individuals decide to trade off sleep and

other behaviours, will further our understanding of behavioural contributions to variation in fitness components in natural populations.

Behavioural sleep may be defined as quiescence in a stereotypical posture with an increased arousal threshold and rapid reversal to wakefulness (Flanigan, 1972; Tobler, 1985). Sleep behaviour has been observed in every species sufficiently studied (Cirelli & Tononi, 2008); however, most work has been done on humans and other mammals, and typically in laboratory settings. Studies comparing sleep patterns measured in the laboratory versus studies of free-living animals have highlighted striking differences in the expression of sleep behaviour between the two conditions (Rattenborg et al., 2008), suggesting that 'normal' behaviour and physiology may not be reflected in laboratory studies (Niemelä & Dingemanse, 2014). Much work has focused on elucidating relationships between abiotic ecological factors, such as temperature and light conditions and components of sleep (Steinmeyer, Schielzeth, Mueller, & Kempnaers, 2010), whereas relatively little work has investigated the effects of ecological factors such as predation risk on sleep in the wild. Although laboratory

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studies provide insights into the basic functions and mechanisms of sleep, studies of variation in sleep behaviours performed under natural, ecologically relevant, conditions are necessary to help further our understanding of the evolution of sleep behaviour (cf. Lesku et al., 2012).

Predation constitutes a major selection pressure; therefore, an individual's antipredator behaviour has major fitness consequences. In certain species, exposure to predation risk correlates with sleep patterns relating to vigilance (peeking rate), posture (Dominguez, 2003; Gauthier-Clerc, Tamisier, & Cezilly, 1998; Lendrem, 1983), total sleep time (Capellini, Barton, McNamara, Preston, & Nunn, 2008) and time spent awake (Lesku et al., 2008). Some species have developed behavioural means of reducing the predation risk associated with decreased responsiveness during sleep by incorporating intermittent bouts of 'peeking' throughout the night (Lendrem, 1984), similar to daytime 'scanning' for predators (Beauchamp, 2009). Plasticity in sleep behaviour as a response to predation risk may help to optimize sleep to the particular risk environment, balancing the gains of sleep with behavioural defence during a particularly vulnerable time. Because both sleep and antipredator vigilance are useful behaviours that are mutually exclusive, we expect a trade-off between the two such that observable variation in sleep patterns should exist as a function of the prevailing predation risk. Here we investigated whether this hypothesized trade-off between vigilance against predation and sleep may underlie variation in sleep patterns in the wild. We therefore studied whether predation risk as a key ecological factor may explain variation in sleep behaviour of individuals.

One approach to assess a trade-off between vigilance and sleep is to experimentally increase or decrease perceived predation risk in an individual's environment. When the probability of a predation event during usual sleep time increases, we might expect individuals to compensate by increasing antipredator vigilance at the cost of quality or quantity of sleep. Typically, studies of predation risk examine the effect of a single predator species (reviewed in Sih, Englund, & Wooster, 1998) or an unspecified source of predation risk (Rattenborg, Lima, & Amlaner, 1999; Roth, Lesku, Amlaner, & Lima, 2006). However, most prey organisms are under pressure from multiple predator species in various environments. For example, birds that roost in cavities are at risk of predation both inside and outside their roosting site from different predator species.

Here, we experimentally increased the risk of predation for individual great tits using models of pine marten, *Martes martes*, and tawny owl, *Strix aluco*. The great tit is an ideal species for the study of avian sleep and behavioural response to predation risk. Great tits roost solitarily and breed in cavities, and readily accept man-made nestboxes as roosting sites which can easily be fitted with experimental equipment to monitor their behaviour at night (see Steinmeyer et al. (2010) for a general description of behavioural sleep during winter in the closely related blue tit, *Cyanistes caeruleus*). The pine marten is a nocturnal and crepuscular (Zalewski, 2001) generalist omnivore that preys most heavily on birds including the great tit during the spring and summer nesting phases. Pine martens are typically active predators that often patrol areas where prey are likely to be found, preying on small birds during the winter when mammalian prey densities are low (Balestrieri et al., 2011; Goszczynski, Posluszny, Pilot, & Gralak, 2007). Martens may attack and prey on adult great tits by entering their roosting cavity, and are known to open the doors and lids of artificial nestboxes. The tawny owl is a sit-and-wait predator that is also nocturnal and crepuscular (Martin, 1990; Sunde, Bolstad, & Desfor, 2003), feeding mostly on mammals and small birds (Jedrzejewski, Jedrzejewska, Szymura, & Zub, 1996,

Jedrzejewski, Jedrzejewska, Zub, Ruprecht, & Bystrowski, 1994) but only outside cavities at night or during twilight and sunrise. Exploring trade-offs between sleep and vigilance from a multiple-predator perspective would contribute to a richer ecological framework from which to understand adaptive trade-offs.

The objective of the current study was to determine whether patterns of vigilance and sleep change depending on the type of predation risk individuals experience in the wild. We hypothesized that when exposed to different predator treatments, individuals would optimize their sleep behaviour in response to increased risk inside versus outside the roost. Using taxidermic predator models, we predicted that individuals exposed to a marten (i.e. increased risk of predation inside the nestbox) would display greater vigilance behaviour, measured as the time spent awake and frequency of nocturnal awakenings, and minimize time spent sleeping inside a nestbox. Conversely, we predicted that individuals exposed to an owl (i.e. increased risk of predation outside the nestbox) would maximize the time spent sleeping inside the nestbox and decrease vigilance behaviour which interrupts sleep. We further investigated evening latency to fall asleep (minutes between entering the nestbox and falling asleep) and morning latency to leave the nestbox (minutes between awakening and exiting the box) as these times may act as a buffer where sleep and waking vigilance may flexibly trade off. These evening and morning latencies may be replaced with sleep after exposure to increased owl predation as sleep may confer greater benefits than rest if birds remain within the box. Latencies may be decreased after exposure to a marten if it is less risky to be outside the box when marten predation risk is increased.

METHODS

Study Species and Study Sites

The experiment was conducted in December 2012 in six nestbox plots of free-living great tits in the area between Herrsching and Starnberg, southwest of Munich, Germany. Great tits in these plots experience predation risk from martens (personal observations). Each field site in the study is a 9–12 ha forested plot with 50 nestboxes installed in 2009. Individuals included in the experiment had been previously captured (January 2010–2012) as part of a long-term study. During the winter, birds roosting in nestboxes were collected at night and brought to the laboratory (see Stuber et al., 2013 for further details) to be measured and implanted with passive integrated transponder (PIT) tags (see Ethical Note) for identification (Nicolaus, Bouwman, & Dingemanse, 2008) before being released at the place of capture following standard protocols (N. J. Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002, 2012). Implanting PIT tags in birds enabled us to record where each bird was roosting while minimizing human disturbance by scanning the outside walls of nestboxes with hand-held PIT-tag readers (Trovan, U.K., www.trovan.com; Steinmeyer et al., 2010).

Experimental Design

In December, all nestboxes in the six plots were inspected at night for the presence of PIT-tagged roosting great tits (as previously described). Birds were semirandomly assigned to either an experimental group ($N = 11$) or an unmanipulated group ($N = 13$) such that each individual was distant enough (>100 m) from the nearest other subject bird to avoid treatment spillover effects. The following day, lids on nestboxes in which PIT-tagged birds had roosted the previous night were exchanged for identical lids that contained a small infrared-sensitive black-and-white, battery-powered camera (S/W-Kamera modul 1, Conrad Electronic, www.conrad.com).

conrad.de). Six LEDs emitting infrared light were placed around each camera objective and used as a light source. Each camera was connected to a digital recorder (AEON—MDVR, Lupus Electronics, Landau, Germany) that saved the recording on an SD card. Recorders and batteries were kept in a waterproof box that was covered in camouflage material and leaves or snow (depending on weather conditions). Cameras were programmed to record from 1600 to 0900 hours to capture each subject's entire sleep duration overnight, including its entering and exiting the nestbox. Memory cards and batteries were changed daily, at least 30 min after removal of the taxidermic model; video recordings were made during all nights of the experiment including 'response' and 'no manipulation' nights (see Table 1).

Novel objects in the nestbox such as recording equipment have contributed to roosting site abandonment by certain behavioural types in the studied population (Stuber et al., 2013). To avoid sampling bias, all nestboxes were fitted with dummy cameras at least 4 months before the experiment (August 2012) to allow for habituation, which reduced nestbox abandonment from approximately 42% (Stuber et al., 2013; abandonment due to introduction of a camera into the nestbox when no dummy camera had been previously fitted: 68 abandoned of 161 birds) to 13% (abandonment after dummy camera had been fitted due to natural nestbox changes or mortality: 22 abandoned of 170 birds). Dummy cameras were replaced with functioning cameras only on filming days. Because great tits exhibit short-term roost site fidelity (estimated 100% over consecutive days; Stuber et al., 2013), we assumed the same individual was recorded in the same nestbox for the duration of the experiment.

We recorded 'baseline' sleep in all birds prior to the start of experimentation (Table 1) to determine the general morning awakening time of all individuals. This morning awakening time was subsequently used to determine what time the experimental treatment should begin for each individual in the mornings. Following the baseline recording, individuals were exposed to two types of taxidermic predator models (pine marten and tawny owl; for photos see Supplementary Material Figs S1–S3) that simulated increased predation risk, and a nonpredator model as a control (blackbird, *Turdus merula*). Blackbird models were used to ensure that individuals were reacting to a predator rather than a novel object or a heterospecific individual in a novel location (Milinski, 1997). Blackbirds do not utilize cavities for roosting or nesting, and therefore do not compete with great tits for access to nestboxes. Within species (four male blackbird models; six tawny owl models, three of each sex; and six pine marten models, three of each sex), the taxidermic models were mounted in approximately the same body position (see photos: Figs S1, S2). Multiple taxidermic models of each species were used to ensure that great tits

were reacting to a predator or nonpredator and not to specific characteristics of a particular model (Hurlbert, 1984). As we predicted that exposure to marten versus owl predator models would elicit responses in opposite directions, we consider each predator type a specific treatment (i.e. marten treatment or owl treatment) rather than both together as a general 'predator' treatment. Birds assigned to the unmanipulated group were not exposed to any taxidermic model.

Fifteen minutes prior to the expected awakening time of the individual (as determined from baseline recordings; see above), a taxidermic model was placed approximately 1 m in front of the entrance to the nestbox and left standing for a total of 45 min prior to removal. After installation, observers left the area. The models were placed such that the bird would see the predator prior to departure from the nestbox. Sleep behaviours of each bird were recorded the following night (i.e. ca. 8 h later).

Each treated individual was given 1 day without an experimental treatment followed by exposure to a different type of taxidermic model (i.e. if the bird was exposed to a marten model, it was then exposed to either an owl or blackbird model; Table 1). The procedure was repeated such that all treated birds were exposed to a marten, an owl and a blackbird model in random order over the course of 8 days. The experiment spanned from 7 December to 16 December, with each day including recordings from both unmanipulated and treated birds; during the experiment we did not experience unseasonably adverse weather conditions (i.e. no heavy rain or snow).

Manipulations of Perceived Predation Risk

We performed a pilot study in November 2012 in a single field site, prior to the experiment, to evaluate the effectiveness of stuffed, taxidermic predator models (Figs S1, S2) in eliciting an anti-predator behavioural response. After locating roosting birds, we selected five individuals (not used in the actual experiment) and exposed them to a marten or owl model at the nestbox on the subsequent morning. Video recordings confirmed that installation of the models prior to a bird's awakening time did not prematurely waken the birds. After installing a taxidermic model in front of a nestbox, an observer hid 15 m from the box and watched with binoculars for 45 min, after which the model was removed. Anti-predator behaviours observed in focal individuals included avoiding exiting the nestbox while the model was present (two individuals), exiting the nestbox with minimal body movement to avoid attracting attention (two individuals) and alarm calls in the vicinity of the box (three individuals). None of the birds approached or attacked the predator model. The pilot thus confirmed that the birds recognized the predator models as a threatening stimulus.

Table 1
Overview of the experimental design

Sequence (night)	Treatment group 1	Treatment group 2	Unmanipulated group 1	Unmanipulated group 2
	Plots 1, 2, 3	Plots 4, 5, 6	Plots 1, 2, 3	Plots 4, 5, 6
0	Baseline	Baseline	Baseline	Baseline
1	No manipulation	No manipulation	Unmanipulated response	Unmanipulated response
2	Response to T1	No manipulation		
3	No manipulation	Response to T1	Unmanipulated response	Unmanipulated response
4	Response to T2	No manipulation		
5	No manipulation	Response to T2	Unmanipulated response	Unmanipulated response
6	Response to T3	No manipulation		
7		Response to T3		Unmanipulated response

Each of six field sites (plots) was randomly assigned arbitrarily to group 1 or 2 such that treatments could be staggered over days; Baseline recordings were made prior to any manipulation and were only used to determine individuals' expected awakening time for taxidermic model placement. Baseline recordings were not included in the statistical analysis. The sequence of treatments (T1, T2, T3) was randomly assigned (blackbird, marten or owl) within each individual. Unmanipulated control individuals, not exposed to any treatments, were filmed on all days. Each day, regardless of treatment or no manipulation, every nestbox was visited to change camera batteries and SD cards.

Furthermore, we analysed videos, made during the experiment, of morning behaviours (number and rate of peeking out of the entry hole, number of times sitting in the entry hole and amount of time between first looking out of the entry hole and exiting the nestbox, all log-transformed for normality) while taxidermic models were present outside their nestbox. These immediate responses to presentation of models provided support for the assumption that individuals saw and recognized models outside their nestbox, and thus support the success of the treatment such that any null results would not be caused by individuals missing or not perceiving the treatment.

Video Recordings

During the course of the experiment, one treatment and one unmanipulated bird abandoned their nestbox before any useful data were recorded, and were subsequently dropped from the analysis. A second treatment bird abandoned its box after being exposed to two predator treatments. We obtained a total of 43 complete recordings. Of the 11 birds (five female, six male) assigned to the treatment group, we obtained 10 recordings of response to marten models, nine to owl models and nine to blackbird models. We obtained 19 recordings from eight birds (seven female, one male) assigned to the unmanipulated group. In all cases, missing data were due to mechanical failures of recording equipment in the field.

To measure sleep-related variables, videos were scored by a single observer (M.G.), who was blind to the identity of the recording. Sleep onset time was defined as the first time the bird placed its head under the scapular feathers (Amlaner & Ball, 1983) and ceased movement for at least 30 s. Awakening time was defined as the end of the final sleep bout lasting at least 30 s. From these data we calculated sleep duration, defined as the duration of time between evening sleep onset and awakening in the morning. We converted sleep duration to sleep duration relative to night length (unitless; reference sunset and sunrise times from the town of Andechs which is near our study sites; sunset range during the experiment 1945–1926 hours, sunrise range during the experiment 0641–0653 hours). We converted sleep onset and morning awakening to minutes relative to sunset (sleep onset; i.e. a bird entering the box 5 min before sunset would be scored as -5) or sunrise (morning awakening; i.e. a bird exiting the nestbox 5 min before sunrise would be scored as -5). Evening latency was defined as the amount of time (min) between entering the box and falling asleep; morning latency was defined as the amount of time (min) between awakening in the morning and leaving the nestbox.

We used a motion detection software program based on the AForgeVision image processing library (aforegenet.com; Surhone, Tennoe, & Henssonow, 2010) further developed at the Max Planck Institute for Ornithology to determine the number of times an individual awoke during the night and the duration of each awakening bout. Based on video recordings of 12 frames/s, the software program calculates changes in pixels between any scene and a background as a 'motion value'. Motion values greater than motion during sleep correspond to waking locomotor activity. Motion values below this threshold correspond to small movements made by the bird (i.e. breathing or the twitch of a feather) or noise. These critical thresholds were determined by visual comparison of video recordings with values of changes in pixilation, and varied with the quality of the video recording. The visually defined onset of an awakening bout during the night was defined as the moment the bird lifted its head from under its wing, and the end of an awakening bout was defined as the moment a bird ceased moving after placing its head under its scapular feathers. Minor

movements such as moving the tail or small adjustments to the wings were not considered 'awake,' as these movements often occurred while the bird was assumed to be asleep. Videos in which the picture quality was too low to be scored by the motion detection software (two of 43 observations) were scored entirely by hand by a single observer (M.G.). We consider these behaviours to be independent variables as they are only weakly correlated (see Supplementary Material Table S1), which suggests that they can vary independently of each other.

Because individuals may alter their use of cavities under different predation risk conditions rather than sleep per se if sleep patterns are inflexible, we investigated nestbox entry time in the evening (minutes relative to sunset), nestbox exit time in the morning (minutes relative to sunrise) and total time spent in the nestbox (min). If sleep needs of individuals are strictly set, birds may alter the likelihood of being preyed at by preferring or avoiding being inside cavities during vulnerable times. Birds may spend more time inside the box when owl predation risk is increased, and avoid being inside boxes when marten predation risk is increased. Total time spent inside the nestbox, and morning exit time were not affected by the treatments (Appendix Table A1). Evening nestbox entry time was similar within the treatment groups, but unmanipulated individuals entered the box earlier in the evening. As this suggests that birds did not alter cavity usage, we focus our attention and discussion on sleep behaviour specifically.

Statistical Analysis

Based on a priori hypotheses, we performed one analysis of sleep behaviour (sleep duration relative to night length), two analyses of vigilant sleep behaviour (frequency of nocturnal awakenings/h and total time spent awake (min) which was log-transformed for normality) and two analyses of nestbox occupancy (evening and morning latency: min). Morning latency was log-transformed to better approximate normality. We constructed linear mixed-effects models for these variables which followed a Gaussian error distribution (package lme4, R 2.14.1; R Development Core Team, 2011). All models contained the same fixed effects: sex (males and females are known to differ in risk-taking behaviour and sleep; Abrahams & Cartar, 2000; Kavaliers & Choleris, 2001; Steinmeyer et al., 2010), sequence (day of exposure within the experimental period; i.e. first, middle or last exposure) and treatment (unmanipulated, blackbird, marten or owl). Individual identity nested within plot, plot and date were all fitted as random effects. Recordings in which individuals were exposed to the nonthreatening blackbird model served as the reference group against which recordings of birds exposed to predators and unmanipulated birds (no exposure to animal models) were compared. We did not use birds from the unmanipulated group as our reference group, as a significant difference in response to treatment with an animal model could represent a response to novelty (presence of something unfamiliar in front of the nestbox) rather than a response to a predator model, specifically. Model estimates of 'Intercept' refer to this blackbird reference group.

To obtain parameter estimates we used the sim function (package arm, R 2.14.1; R Development Core Team, 2011) to simulate values from the posterior distributions of the model parameters. Based on 5000 simulations, we extracted 95% credible intervals (CI) around the mean (Gelman & Hill, 2007), which represent the uncertainty around our estimates. We consider an effect to be 'significant' in the frequentist sense if zero is not included within the 95% CI. We used visual inspection of residuals to assess model fit. We also calculated the conditional R^2 , as an absolute measure of goodness-of-fit of each model following Nakagawa and Schielzeth (2013).

We calculated the adjusted individual repeatability (i.e. repeatability after correcting for all fixed and random effects; Nakagawa & Schielzeth, 2010) of behaviours as the between-individual variance divided by the sum of the between-individual and residual variances of the random effect of individual identity based on simulations (described above). Repeatability calculations were based on all experimental data included in the models, between days and including exposure to all treatments.

Ethical Note

The individuals used in this experiment were all previously marked birds, as they are part of a larger, long-term project. In our study populations, birds have been collected and marked since 2010 with PIT tags (Destron Fearing, MN, U.S.A., model: TX148511B, 8.5×2.12 mm, <0.1 g, approximately 0.6% of body weight). Birds were caught inside nestboxes at night while roosting (i.e. without traps); all personnel involved in training others in collecting and handling birds were covered under experimental permits and everyone involved in handling underwent thorough training with supervision of senior team members. After collection, birds were housed in the laboratory overnight for less than 24 h for measurement before tagging (implantation protocol following Nicolaus et al., 2008; Regierung von Oberbayern permit no. 55.2-1-54-2532-140-11). Following a similar protocol, Dingemanse et al. (2002) did not observe any adverse effects of this stay outside their natural environment on body weight and mortality, or loss of territory (when performed during the breeding season). Using tags of similar size and dimension (Trovan ID100, implantable PIT tags), Nicolaus et al. (2008) demonstrated that subcutaneous implantation of PIT tags did not negatively influence survival or recruitment of great tits and breeding success of adult birds captured and implanted during winter was not affected by presence of a PIT tag. An individual's state of health is assessed in the laboratory after collection for potential exclusion from measurements; during the holding period, only one bird was excluded from measurement for health reasons (escaped capture and collided with a window). No birds were injured during collection or handling. Of the 510 individuals collected, only two died between capture and release from the laboratory, which is well within the natural range of this species (great tit annual mortality is approximately 0.5; Bauchau & van Noordwijk, 1995; see also ethical note in N. J. Dingemanse et al., 2002).

We were unable to track the movement of birds that abandoned their boxes during this experiment; however, the rate of nestbox abandonment was within the normal range of this population due to its somewhat transient nature and these individuals were all recorded alive in the field sites at a later date. Permits were obtained from the Bavarian government and the Bavarian regional office for forestry LWF (permit no. 55.2-1-54-2532-140-11).

RESULTS

Immediate Response to model Presence

During model presentations in the morning individuals observed the models placed outside their nestboxes and, compared with unmanipulated controls, significantly increased the absolute number of 'peeks' out of the nestbox entrance, the absolute number of times sitting in the nestbox entry hole and the amount of time (min) before leaving the nestbox after first peeking out of the entrance (37 observations of 19 individuals; see Table 2). Frequency of peeking/h was similar between unmanipulated individuals and those exposed to blackbird and marten models; individuals exposed to owl models increased the frequency of peeking per unit time (Table 2). The time between an individual's awakening and first peek out of the box entrance was not different between the unmanipulated and treatment groups, confirming that our physical placement of the taxidermic models at the site of the nestbox did not disturb the birds' normal sleep pattern (Table 2).

Sleep 1 Night after Presentation of Models

Comparison of control groups

We explored differences in sleep behaviours between the unmanipulated group and the blackbird treatment (the presumed nonthreatening control in the treated group; 'effects of intercept (bb)', in Table 3) on the night after taxidermic model presentation. We detected a strong effect of exposure to blackbird treatment on frequency of awakenings/h. Compared with birds exposed to the blackbird model, birds in the unmanipulated group woke up less frequently during the night following the presentation (Table 3). The frequency of nocturnal awakenings could have been affected by the appearance of a nonthreatening heterospecific in a novel location, directly in front of the nestbox, disturbance created by placement of the taxidermic model during the previous morning or long-term effects of exposure to prior experimental treatments (for those birds that did not receive the blackbird treatment first). Evening sleep latency was longer in unmanipulated birds than in birds exposed to the blackbird model (Table 3). Other sleep behaviours were not significantly different between the unmanipulated and blackbird treatment groups.

Treatment effects

Morning exposure to predator treatments caused changes in sleep behaviours the following night; as expected, the effect depended on the particular predator species treatment (Table 3). Birds exposed to marten models altered sleep patterns such that they woke up less often during the night compared with exposure to the blackbird reference (Table 3, Fig. 1; model conditional $R^2 = 0.76$). Individuals exposed to an owl model slept relatively

Table 2
Immediate response to taxidermic model presentation during time of presentation

	No. of peeks out of entry hole			No. of times sitting in entry hole			Exit latency			Peeking frequency			Awakening to 1st peek		
	β	$q^{2.5}$	$q^{97.5}$	β	$q^{2.5}$	$q^{97.5}$	β	$q^{2.5}$	$q^{97.5}$	β	$q^{2.5}$	$q^{97.5}$	β	$q^{2.5}$	$q^{97.5}$
Intercept	1.57	0.90	2.25	0.61	0.03	1.18	0.29	-0.48	1.07	-1.16	-1.70	-0.62	0.47	-0.12	1.06
Treatments															
Blackbird	1.90	1.07	2.74	1.13	0.46	1.8	2.36	1.38	3.31	0.48	-0.15	1.15	0.30	-0.58	1.16
Marten	1.80	1.02	2.55	0.95	0.36	1.55	2.41	1.54	3.29	0.47	-0.13	1.12	0.40	-0.41	1.26
Owl	1.90	1.11	2.69	0.82	0.18	1.45	2.96	2.05	3.90	0.94	0.30	1.60	0.58	-0.27	1.44

The table shows fixed-effects parameter estimates of linear mixed-effects models of morning behaviour. Values are reported with 95% credible intervals. Values for the intercept represent estimates from 'unmanipulated' individuals that did not receive a taxidermic model. β is the estimated coefficient (mean of the posterior distribution). $q^{2.5}$ and $q^{97.5}$ = 2.5% and 97.5% quantiles of the posterior distribution (95% credible intervals). Effects with credible intervals that do not include zero are considered 'significant' and printed in bold.

Table 3
Sleep response to taxidermic model presentation ca. 8 h after presentation

	Relative sleep duration ^a			Frequency of awakenings			Time spent awake (min)			Evening latency (min)			Morning latency (log min)		
	$\beta/\sigma^2/r$	q ^{2.5}	q ^{97.5}	$\beta/\sigma^2/r$	q ^{2.5}	q ^{97.5}	$\beta/\sigma^2/r$	q ^{2.5}	q ^{97.5}	$\beta/\sigma^2/r$	q ^{2.5}	q ^{97.5}	$\beta/\sigma^2/r$	q ^{2.5}	q ^{97.5}
Fixed effects															
Intercept (bb)	0.982	0.967	0.998	6.15	4.75	7.62	39.77	27.6	51.54	2.44	1.40	3.47	2.06	1.20	2.96
Unmanipulated	0.005	−0.005	0.015	−1.93	−3.05	−0.81	0.35	−6.32	7.04	1.25	0.21	2.37	−0.31	−1.18	0.54
Sex	−0.001	−0.009	0.008	−0.88	−1.86	0.08	−4.33	−10.26	1.74	0.66	−0.23	1.58	−0.27	−1.08	0.53
Sequence	−0.002	−0.006	0.001	−0.03	−0.35	0.28	−1.42	−3.67	0.78	−0.01	−0.17	0.15	−0.07	−0.20	0.06
Treatments															
Marten	0.008	−0.001	0.017	−0.87	−1.70	−0.08	0.54	−4.98	6.05	−0.09	−0.95	0.75	0.09	−0.42	0.59
Owl	0.011	0.002	0.02	−0.05	−0.93	0.85	−2.50	−8.15	3.07	0.44	−0.42	1.29	−0.24	−0.79	0.39
Variances															
Individual	0.030	0.012	0.05	0.52	0.24	0.80	6.01	2.91	9.99	0.50	0.25	0.81	0.41	0.21	0.63
Plot	0.010	0.000	0.02	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.01	0.22
Date	0.061	0.018	0.11	0.49	0.13	0.94	18.86	8.23	30.76	0.00	0.00	0.00	0.04	0.00	0.09
Residual	0.059	0.036	0.09	0.50	0.29	0.73	9.07	5.01	13.38	0.66	0.40	0.95	0.22	0.12	0.32
Repeatability	0.33	0.2	0.47	0.5	0.38	0.64	0.43	0.24	0.52	0.49	0.29	0.55	0.65	0.52	0.77

The table shows fixed-effects parameter estimates of linear mixed-effects models of sleep behaviour and estimates of random-effects variances and adjusted repeatability. Values are reported with 95% credible intervals. Values for the intercept represent estimates from the blackbird treatment group (bb). $\beta/\sigma^2/r$ indicates the estimated coefficient (mean of posterior distribution; β for fixed effects, σ^2 for variances and r for repeatability). q^{2.5} and q^{97.5} = 2.5% and 97.5% quantiles of the posterior distribution (95% credible intervals). Estimates with credible intervals that do not include zero are considered 'significant' and printed in bold. (bb) = estimates of intercepts refer to exposure to blackbird taxidermic models.

^a Variance estimates have been multiplied by 1000 for visualization.

longer (Table 3; this corresponds to an increase of approximately 10 min; model conditional $R^2 = 0.69$) compared with the blackbird reference (Fig. 2).

Main effects of sex, and treatment sequence, were never significant predictors of behaviours in response to predator presence. After exposure to marten and owl taxidermic models, birds did not alter their total time spent awake during the night, or evening or morning sleep latency (Table 3; time spent awake, evening latency, morning latency model conditional $R^2 = 0.77$, 0.56, 0.75, respectively).

We found support for relatively high day-to-day adjusted individual repeatability in frequency of awakenings, total time spent awake and evening and morning latency (based on our full models which account for treatment effects) and moderate individual repeatability in relative sleep duration (Table 3). Differences between plots explained little variation in these behaviours (Table 3).

Sleep duration, frequency of awakenings/h and time spent awake also varied considerably between days (Table 3).

DISCUSSION

Although it is well accepted that sleep plays an important role in an individual's survival and performance capabilities, it is relatively understudied in behavioural ecology (Steinmeyer et al., 2010). Despite the importance of sleep, sleep patterns may be constrained by ecological factors such as the prevailing predation risk, temporal limitations on optimal foraging opportunities and reproductive competition. Our study experimentally demonstrates that great tits adjust specific sleep and vigilance behaviours in response to different sources of predation risk. When exposed to increased perceived predation risk inside the roost site, individuals on average woke less often during the night, but did not alter total

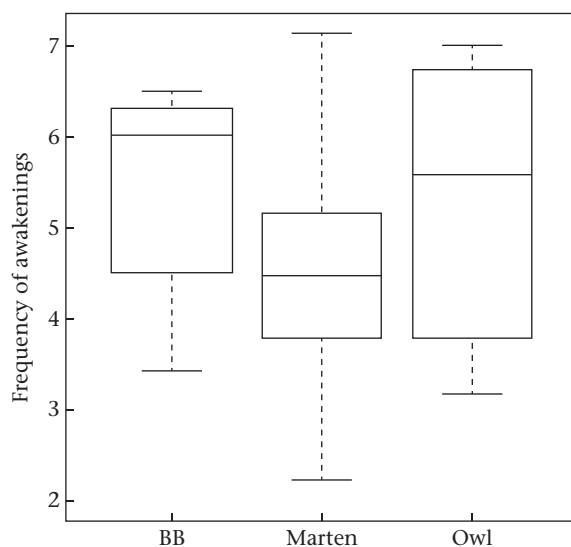


Figure 1. Raw data frequency of night-time awakenings/h versus treatment (mean \pm SD; blackbird: 5.37 ± 1.23 ; marten: 4.52 ± 1.36 ; owl: 5.30 ± 1.71). The box plot represents the interquartile range of the data; the line inside each box represents the median and the whiskers extend to $1.5 \times$ interquartile range.

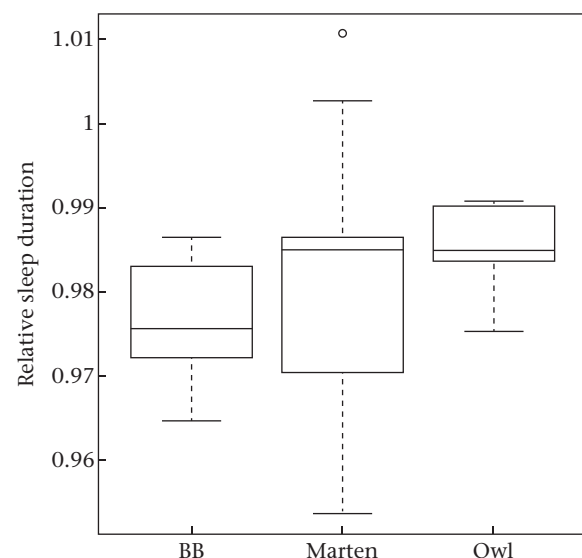


Figure 2. Raw data relative sleep duration (duration of sleep relative to night length) versus treatment (mean \pm SD; blackbird: 0.977 ± 0.008 ; marten: 0.983 ± 0.017 ; owl: 0.985 ± 0.006). The box plot represents the interquartile range of the data; the line inside each box represents the median and the whiskers extend to $1.5 \times$ interquartile range. The circle indicates a point outside this range.

time spent awake during the night. When exposed to increased perceived predation risk outside the roost site, individuals, on average, slept 10 min longer. We have shown short-term behavioural plasticity in response to changes in predation risk from opposing sources; however, it is also important to investigate the potential for long-term or carryover effects of increased perceived predation risk on sleep behaviour.

Following treatment with increased owl predation risk birds slept significantly longer. These results are in line with our hypothesis that under increased risk of predation outside the nestbox (at times of increased owl predation risk) birds should maximize the time spent inside the nestbox sleeping. It is unclear whether in this situation an increase of 10 min to sleep duration confers measurable physical or cognitive benefits. However, in humans, naps of 10 min following 1 day of sleep restriction confer significant improvements to alertness and cognitive performance (Brooks & Lack, 2006; Tietzel & Lack, 2002) while brief naps of 15 min improve task performance in humans after normal sleep (Takahashi, Fukuda, & Arito, 1998). Sleep conserves more energy than quiet rest (Berger & Phillips, 1995; Jung et al., 2011) and if birds decide to stay inside the nestbox where it is presumably safer, it might be more beneficial to spend that time sleeping rather than resting. We can only speculate on potential trade-offs between sleep behaviour and daytime behaviours occurring outside the nestboxes as we did not record any daytime, out-of-box behaviours. Furthermore, increasing owl predation risk did not elicit a change in frequency of awakenings or time spent awake during the night after exposure. These results are in line with the hypothesis that individuals should not trade sleep for vigilance when roosting inside the nestbox is less risky than being outside.

Contrary to our expectation, increasing marten predation risk did not decrease birds' sleep duration during the night following exposure. There are several potential explanations for this. First, minimum sleep requirements may constrain individuals such that decreasing sleep time would be maladaptive. Second, because martens are common in the study area, individuals might already have adjusted their sleep behaviour, independent of the experiment. However, experimental treatment with a pine marten at the roost location did cause birds to wake up less frequently during the following night. This may seem counterintuitive, as this suggests that birds are less vigilant. Considering an average winter sleep duration of approximately 15 h, even a reduction in frequency of awakenings from 6.15 (under nonpredator conditions) to 5.28 (after marten exposure) awakenings/h translates to an absolute difference of approximately 92 total awakenings per night versus 79. The biological relevance of such a difference has yet to be investigated. We speculate that waking less frequently might be adaptive if it reduces noise production, making individuals less conspicuous during the night ('acoustical avoidance': Curio, 1976; Ruxton, 2009). Alternatively, these individuals may be more sensitive to physical disturbances of the nestbox than to predator movement in the environment surrounding the nestbox. These hypotheses warrant experimental verification. It is interesting that individuals did not decrease their time spent awake; this result may arise if birds suppress only the very short (ca. 1 min) nonrhythmic awakening bouts that occur at the beginning of the night, rather than the long, rhythmic awakening bouts that occur throughout the night (Mueller, Steinmeyer, & Kempenaers, 2012). These unexpected effects underscore the importance of experimental field studies in generating appropriate hypotheses concerning the ecology of sleep.

Individuals did not alter evening or morning latencies when exposed to either predator model. Although we expected birds exposed to increased marten risk to decrease sleep latencies (and therefore minimize time spent inside the cavity not sleeping) we cannot discount the possibility that individuals spent more time in

vigilant rest before entering the nestbox in the evening. Alternatively, it is possible that evening and morning latencies are already minimized by constraints on optimal foraging times and thermoregulatory benefits which we did not test in this experiment.

Individual Repeatability

All behaviours recorded showed individual repeatability which could be caused by genetic differences, environmental factors with long-lasting effects ('permanent environment effects') or individual repeatability in environmental conditions with short-term effects ('environmental effects'; Falconer, 1989). Individuals may experience long-term carryover effects in response to presentations of single predators, or inhabit a particular nestbox that is exposed to a relatively unchanging amount of natural predation risk which would contribute to repeatability of behaviour. Furthermore, repeatability in response to perceived predation risk may come about via differences in cognitive ability (Dukas & Kamil, 2000) if individuals differed in their sensory processing capabilities, individual coping styles or personality (Mathot, Wright, Kempenaers, & Dingemanse, 2012; Niemelä, DiRienzo, & Hedrick, 2012; Sih & Del Giudice, 2012) or if there were habitat-specific differences in actual predation pressure. These repeatability estimates in great tits are generally comparable to those measured in blue tits; however, our estimates for evening and morning latency were higher (great tits: $r = 0.49, 0.65$, respectively; blue tits: $r = 0.26, 0.38$, respectively; Steinmeyer et al., 2010; although note that our model structure differed from that presented in a study of blue tits which is known to affect repeatability: Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010; Steinmeyer et al., 2010).

Effects of Model Presentations per se

Results from the evaluation of the birds' behaviour while a taxidermic model was present (immediate response to physical presence of the model in the morning) assured us that individuals perceived the treatment as something out of the ordinary, and thus acted differently while the objects were present outside their box. This lends strength to our assumption that null results can be considered true nonresponses, rather than the result of birds not perceiving the treatment as a treatment (i.e. a failed experiment). It is possible that we were unable to detect some treatment effects because the strength of the treatment was too weak (i.e. treatment effects from exposure to a taxidermic model in the morning did not last until the following night when sleep responses were measured). However, we believe that increasing the strength of the treatment may lead to more nestbox abandonment either immediately or cumulatively over the course of repeated exposure. Future studies could aim to quantify the consequences of changes in sleep and vigilance after longer-term exposure to predation risk or by comparing sites that differ in the presence or density of specific predator species.

The experimental design of our study incorporated two layers of control groups: the blackbird treatment and the unmanipulated group. A within-individual sampling design in which an individual can act as its own control theoretically increases the power of the study such that a relatively smaller sample size can be utilized (Seltman, 2010). We decided to record the behaviour of an additional unmanipulated group, not exposed to any treatment, to statistically account for day-to-day variation in sleep behaviour under 'natural' conditions and thereby further improve our statistical power to detect treatment effects. Such daily variation was indeed considerable in all behaviours except evening and morning latency.

Comparing unmanipulated birds with the blackbird treatment also allowed us to test potential effects of novelty of the treatment. We expected that the sleep behaviours of the unmanipulated group would match the response of individuals when exposed to the nonthreatening blackbird treatment. However, this was not the case when evaluating frequency of night-time awakenings or evening latency to sleep. This could indicate that there is a novelty effect on treatment birds of exposure to something unfamiliar outside their nestbox (see also Mutzel et al., 2013). Alternatively, this could be caused by increased human disturbance at the treated nestboxes as these boxes were visited more frequently to place and remove taxidermic models. Ideally, in future studies, unmanipulated birds should be visited by experimenters as often as the treatment birds.

Conclusions

Animals living in complex environments in which exposure to predation risk is variable should balance trade-offs between necessary behaviours promoting survival and exposure to predation. Earlier studies of individuals' sleep response to predation risk have highlighted plasticity in behavioural responses, but the extent to which this plasticity could reflect the prevailing predation landscape is unresolved. Our results reveal that individuals display consistent differences in behaviours related to sleep, and can actively adjust their behavioural response to immediate, and even opposing, sources of predation risk. Our study demonstrates that individuals manage exposure to increased predation risk by modifying both sleep and vigilance behaviours. Our study also generated unexpected results, supporting the importance of conducting field-based studies to assess the legitimacy of a priori predictions and evaluate spurious findings that may arise from measurement in artificial or laboratory conditions. Such field studies are able to generate new hypotheses and elucidate novel ecological underpinnings of behaviour. As advances are made to other electrophysiological recording equipment, such as those that can create electroencephalograms, it would be interesting to investigate potential changes in quality or depth of sleep, in response to predation pressure, rather than sleep duration; individuals may be able to compensate for changes to sleep quantity with quality. Further research integrating ecology, genetics and sleep and vigilance behaviour promises advances in our understanding of time allocation and trade-offs in individuals utilizing different behavioural strategies to maximize fitness.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2014.10.010.

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Appendix

Table A1

Estimates of nestbox usage parameters measured the night following treatments

	Entry time			Exit time			Time in nestbox (min)		
	β	$q^{2.5}$	$q^{97.5}$	β	$q^{2.5}$	$q^{97.5}$	β	$q^{2.5}$	$q^{97.5}$
Fixed effects									
Intercept (bb)	5.12	−4.74	15.43	−0.01	−11.92	11.79	928.2	912.04	944.53
Unmanipulated	−9.51	−17.3	−1.62	−9.45	−18.96	0.04	1.04	−9.14	11.29
Sex	−4.17	−10.7	2.3	−7.99	−16.06	0.16	−2.8	−11.76	6.14
Sequence	1.34	−0.7	3.35	0.03	−2.57	2.68	−1.09	−4.9	2.56
Treatments									
Marten	−6.04	−12.32	0.11	−3.35	−10.65	3.92	4.41	−4.47	13.24
Owl	−3.21	−9.49	3.24	1.27	−6.41	8.94	6.12	−3.41	15.68

β is the estimated coefficient (mean of the posterior distribution). $q^{2.5}$ and $q^{97.5}$ = 2.5% and 97.5% quantiles of the posterior distribution (95% credible intervals). Both entry and exit times are presented as minutes relative to sunset, and sunrise, respectively. Effects with credible intervals that do not include zero are considered 'significant' and are printed in bold.